

# A NEW SPECIES OF *NEMATOLAMPAS* (CEPHALOPODA: OEGOPSIDA) FROM THE WESTERN CENTRAL ATLANTIC WITH AN OVERVIEW OF THE FAMILY LYCOTEUTHIDAE

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## ABSTRACT

A new squid species of the family Lycoteuthidae, *Nematolampas venezuelensis* is recognized from the central western Atlantic Ocean. The new taxon is characterized by the threadlike, greatly elongated ventro-lateral arms and the presence of a single, large photophore embedded in the musculature of the fin/mantle complex. An overview of the Family Lycoteuthidae is presented based on the examination of the holotypes of *Nematolampas regalis* and *Oregoniateuthis springeri*, reported specimens of *Selenoteuthis scintillans* and *Lampadioteuthis megaleia*, and a review of the literature on the family.

Among the cephalopods collected during the four cruises of the R/V DR. FRIDTJOF NANSEN off the coasts of Venezuela in 1988, were four lycoteuthid squids with very elongated, threadlike ventro-lateral arms. Gross anatomical features initially suggested that the specimens were attributable to *Nematolampas regalis* Berry, 1913. However, closer examination revealed distinctions from Berry's definition of *N. regalis*, and showed them to represent a new species from the central western Atlantic Ocean (Arocha, 1991).

The Family Lycoteuthidae is poorly known due to the lack of sufficient comparative material that would enable a full review. However, in the past decade several advances have been made. There have been important collections of lycoteuthid species made off New Zealand in the southwest Pacific (Förch and Uozumi, 1990) and Namibia in the southeast Atlantic (Villanueva and Sanchez, 1993), that have led to the clarification of the *Lycoteuthis diadema* problem (Toll, 1983; see 'Discussion'). In addition, the type specimens for *N. regalis* and *Oregoniateuthis springeri* Voss, 1956, and previously reported specimens of *Selenoteuthis scintillans* Voss, 1958 and *Lampadioteuthis megaleia* Berry, 1916 were available for examination in the present study. These circumstances, together with a review of the literature, enabled the comparison of the morphological characters of the recognized species and allowed a clarification of the classification of the family members.

Measurements and indices are as defined by Roper and Voss (1983). The following abbreviations are used: USNM, U.S. National Museum of Natural History; UMML, Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami; the R/V NANSEN, is a fisheries research vessel from Norway.

Family LYCOTEUTHIDAE Berry, 1914

Subfamily Lycoteuthinae Pfeffer, 1908

Genus *Nematolampas* Berry, 1913

*Diagnosis.*—Lycoteuthid with ventro-lateral (III) arms longer than mantle, devoid of suckers in distal part of arms in males (females not known). Photophores present near tips

the four dorsal arms and along the entire length of the ventro-lateral (III) arms. Ten photophores within mantle cavity. Males with single genitalia.

*Type species*.—*Nematolampas regalis* Berry, 1913.

*Nematolampas venezuelensis* new species

(Figures 1–4, Tables 1,2)

*Material Examined*.—Holotype: One male, mantle length 87.5 mm, R/V NANSEN sta 1143, northeast of Golfo Triste, Venezuela, 10°55'N, 67°57'W, 371–383 m, bottom trawl, December 2, 1988, USNM 817596. Paratypes: One male, mantle length 67.7 mm, R/V NANSEN sta 1129, off Punta Chuspa, Venezuela, 11°02'N, 62°21'W, 355–365 m, bottom trawl, November 28, 1988, UMML 31.3143. Two males, mantle lengths 65.0 and 58.2 mm, R/V NANSEN sta 146, south of Los Hermanos Islands, Venezuela, 11°20'N, 64°26'W, 298 m, bottom trawl, February 19, 1988, UMML 31.3144.

*Comparative Material*.—*Nematolampas regalis*. Holotype, One male, mantle length 32 mm, R.S. BELL, on beach Sunday Island, Kermadec Island Group-New Zealand, 1910, USNM 815721. Paratype, one male, mantle length 26 mm, R.S. BELL, on beach Sunday Island, Kermadec Island Group-New Zealand, 1910, USNM 816592. *Lycoteuthis springeri*. Holotype, One male, mantle length 80.0 mm, R/V OREGON sta 382, 29°11.5'N, 88°7.5'W, 367 m, June 21, 1951, USNM 575090. One male, mantle length 97.0 mm, R/V OREGON sta 3296, 28°36'N, 89°48'W, 439–936 m, August 21, 1961, UMML 31.376. One female, mantle length 124 mm, R/V COLUMBUS ISELIN sta 256, 23°37'N, 77°6'W, 1360 m in stomach of *Synaphobranchus brevidorsalis*, November 1, 1974, UMML 31.1735. One female, mantle length 62 mm, R/V OREGON sta 481, 28°57'N, 88°40.5'W, 378 m, September 7, 1951, UMML 31.174. Two females, mantle length 48–56 mm, R/V SILVER BAY sta 1198, 24°11'N, 83°31'W, 360 m, June 9, 1959, UMML 31.228. *Selenoteuthis scintillians*. One male, mantle length 17 mm, R/V COLUMBUS ISELIN sta 206, 23°44.2'–23°46.0'N, 81°21.5'–81°24.5'W, 10TKMT, 80 m, February 19–20, 1974, UMML 31.2271. One female, mantle length 26 mm, R/V GILLISS sta 25, 20°26.5'N, 83°57'W, 4383 m, July 23, 1972, UMML 31.1503. two females, mantle length 29–30 mm, R/V OREGON sta 2191, 25°11'N, 89°50'W, 3240 m, May 23, 1958, UMML 31.227. *Lampadioteuthis megaleia*. One male, mantle length 31 mm, DANA sta 4173, 40°46'N, 18°35'W, 400 m, June 3, 1931, UMML 31.2968.

*Diagnosis*.—Lycoteuthid with greatly elongated, ventro-lateral arms in males (females not known), with threadlike distal portions, which are devoid of suckers. Ten photophores on viscera; numerous photophores on dorso- and ventro-lateral arms, head and mantle; five photophores arranged in one row on the ventral periphery of each eye. A single, large photophore embedded in musculature of fin/mantle complex near the base of tail, and on dorsal side, five beadlike photophores serially arranged on elongated posterior end of mantle.

*Description*.—Known only from immature males, largest 87.5 mm ML. Mantle moderately stout, cylindro-conical, tapering posteriorly to a narrow pointed tail; mantle width about one third of length (MWI 26.0–34.0–37.3); anterior dorsal margin slightly produced; ventral margin somewhat indented beneath funnel (Fig. 1). Fins large, muscular and sharply angled laterally, anterior margin convex, concave posterior margin terminally narrows and extends along elongated end of mantle. Combined width about equal

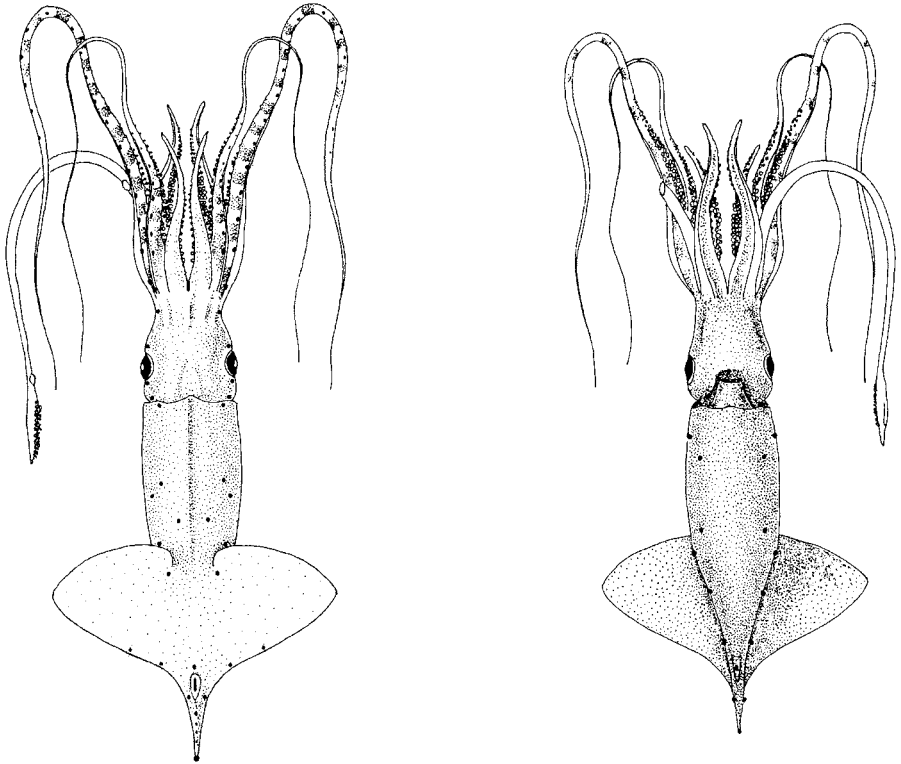


Figure 1. *Nematolampas venezuelensis* n. sp. Dorsal and ventral view (87.5 mm–ML, holotype).

to mantle length (FWI 74.7–84.6–96.6) and length about one third of mantle length (FLI 33.9–36.4–38.8). Anterior fin margins thin with conspicuous notch where they fuse to mantle; posterior margins thick (Fig. 1).

Gladius narrow and darkly pigmented (Fig. 2). Rachis narrow anteriorly (RWI 4.6–4.6–6.2), with straight convergent margins and forming dorsally a strong keel. The vanes are hourglass shaped being slightly widened in midsection, then constricted and posteriorly slightly expanded. The posterior tip of gladius is missing, although it appears to terminate in a cup-shape conus.

Funnel large and stout with two large dorsal supports, anterior quarter projects free of head. Mantle locking apparatus composed of simple, straight funnel member and corresponding slightly raised ridge on inner surface of mantle. Funnel organ indistinguishable in available specimens.

Head moderate in size, rounded, flat dorsally and slightly excavated ventrally; eyes large (EDI 18.3–19.7–21.5), eyelids with well-defined anterior sinus. Ventral surface of each eyeball has five photophores arranged in a single row (Fig. 3A), round central one clearly the largest, remaining four round and small, all with distinct reddish hue.

Arms unequal in length, in order  $3 > 2 > 4 > 1$  except in smallest specimen (Table 1). Dorsal pair of arms with slight fleshy median ridge on distal halves. Dorso-lateral pair almost as long as mantle (ALI II 80.3–92.5–119.8), keeled on proximal half, and attenuated distally into filament. Proximal third of each dorso-lateral arm bears nine equally

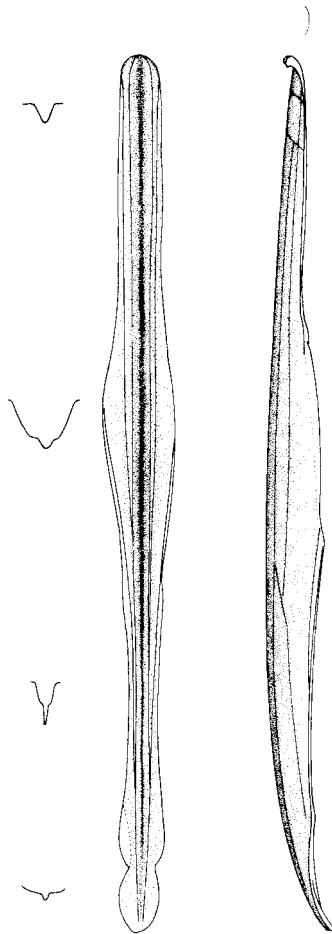


Figure 2. *Nematolampas venezuelensis* n. sp. Gladius, dorsal view with cross sections and side view (87.5 mm–ML, holotype).

spaced round light organs arranged aborally in single series embedded in dermal layer of skin. Ventro-lateral arms more than  $1\frac{1}{2}$  times length of mantle (ALI III 171.4–178.3–191.9), keeled on proximal third and distally attenuated to threadlike filament. Proximal two thirds of each arm bears 19 equally spaced, round light organs arranged aborally in single series as on dorso-lateral arms. Protective trabeculate membranes on suckered portions of all arms. Arms II and III devoid of suckers on filamentous distal portions. Arm suckers stalked, hooded and biserial. Chitinous rings of suckers on midportions of arms with 9–12 sharp teeth on distal border, proximal edge with bluntly pointed teeth (Fig. 3B). Ventral pair of arms strongly keeled. Hectocotylus absent in available males, all immature.

Tentacles, severed in all specimens except the holotype in which the left tentacle remained, long (TtLI 125.7), stout, thick and fleshy at base, attenuate for distal two-thirds. Single available club in poor condition; aboral surface with well-developed swimming keel extending from dactylus to distal part of manus; oral surface bordered by trabeculate

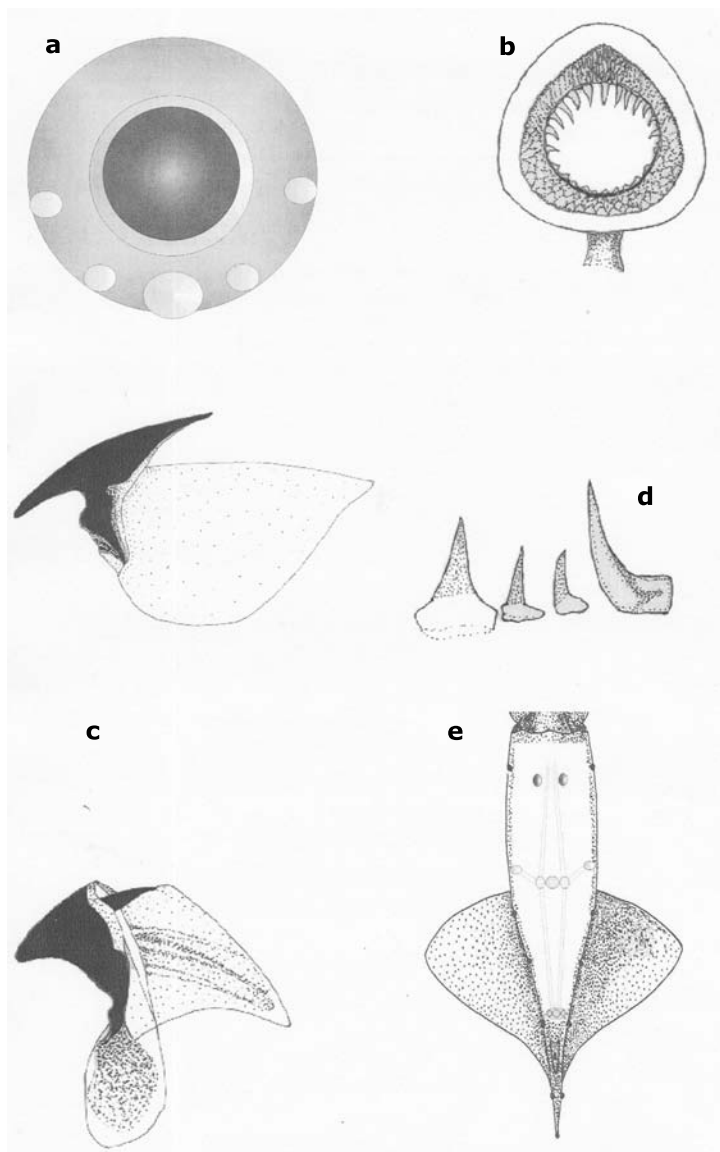


Figure 3. *Nematolampas venezuelensis* n.sp. A) photophore pattern on eye (87.5 mm–ml, holotype); B) large sucker from basal portion of arm IV (87.5 mm–ml, holotype); C) Upper mandible and lower mandible (69.7 mm–ML); D) radular teeth of one side (69.7 mm–ml); E) Internal photophore pattern and connective tissue (87.5 mm–ml, holotype).

protective membranes. Suckers on carpus in four series. Manus and dactylus with small suckers in four series. Two large photophores embedded on oral surface of tentacular stalk, one at about one quarter the length of tentacle and second at base of club.

Buccal membrane reddish purple in preserved specimen, with eight lappets and eight connectives, attached dorsally to arms I, II and IV, ventrally to III; oral surface thickly covered with fleshy papillae. Beaks are as illustrated (Fig. 3C). Lower beak with thick ridge bisecting lateral wall; dark spot near posterior base of each lateral wall evident in

Table 1. Mantle length and indices of type specimens of *Nematolampas venezuelensis* new species.

|            | UMML31.3144 |         | UMML31.3143 | USNM 817596 |
|------------|-------------|---------|-------------|-------------|
|            | Paratypes   |         |             | Holotype    |
| ML         | 58.2 mm     | 65.0 mm | 69.7 mm     | 87.5 mm     |
| Index      |             |         |             |             |
| MWI        | 35.4        | 37.2    | 37.3        | 26.0        |
| HLI        | 23.2        | 18.9    | 18.2        | 16.8        |
| HWI        | 22.9        | 22.0    | 18.5        | 23.7        |
| EDI        | 18.9        | 20.0    | 21.5        | 18.3        |
| FLI        | 36.4        | 38.8    | 33.9        | 36.3        |
| FWI        | 96.6        | 79.7    | 87.5        | 74.7        |
| ALI        |             |         |             |             |
| I          | 59.3        | 41.5    | 41.6        | 30.3        |
| II         | 119.8       | 80.3    | 81.8        | 88.0+       |
| III        | 191.9       | 111.3+  | 172.9       | 171.4       |
| IV         | 49.7        | 45.9    | 42.6        | 38.9        |
| AL formula | 3:2:1:4     | 3:2:4:1 | 3:2:4:1     | 3:2:4:1     |
| TtLI       | -           | -       | -           | 125.7       |
| CLI        | -           | -       | -           | 22.4        |
| GLI        | 96.4        | 86.2    | 84.7        | 74.3        |
| GWI        | 11.5        | 7.7     | 7.9         | 4.9         |
| RWI        | 6.2         | 5.1     | 4.6         | 3.9         |

lower beak of 69.7 mm–ML. Radula as shown in figure 3D, with homodont teeth; marginal plates absent.

Outer integument almost intact in type specimen at capture. Head bears eight photophores: two at bases of third arms, one on either side on dorsal surface near posterior margin of head, one small photophore at anterior edge and another at posterior edge of each eyelid. On dorsal surface of mantle, anterior to fins, integument bears five pairs of photophores. On dorsal surface of fins, integument bears three pairs of photophores, two pairs on dorsal posterior margins of fins, and one pair on anterior end of fin insertion on mantle. On the ventral surface of mantle, six pairs of photophores are present near or along lateral margins.

On the fin/mantle complex, one large photophore lies in pocket in musculature at base of tail, postero-dorsal to conus of gladius. Opening in musculature dorsal to photophore covered by translucent connective tissue that forms a dorsally directed window; three small photophores are found around translucent tissue. Five round photophores deeply buried in dorsal midline of tail terminating in teardrop-shaped organ at distal extremity. One pair of closely set photophores present laterally near midpoint of tail and one photophore ventral to embedded large photophore.

Photophores within the mantle cavity consist of two round anal photophores, one on each side of the anal opening, a set of three abdominal photophores lying transversely on the visceral mass, and one elongate photophore at the base of each gill. A complex of three photophores are located transversely in the posterior ventral mantle fastened to the inner wall of the mantle. All photophores within the mantle cavity are connected by a

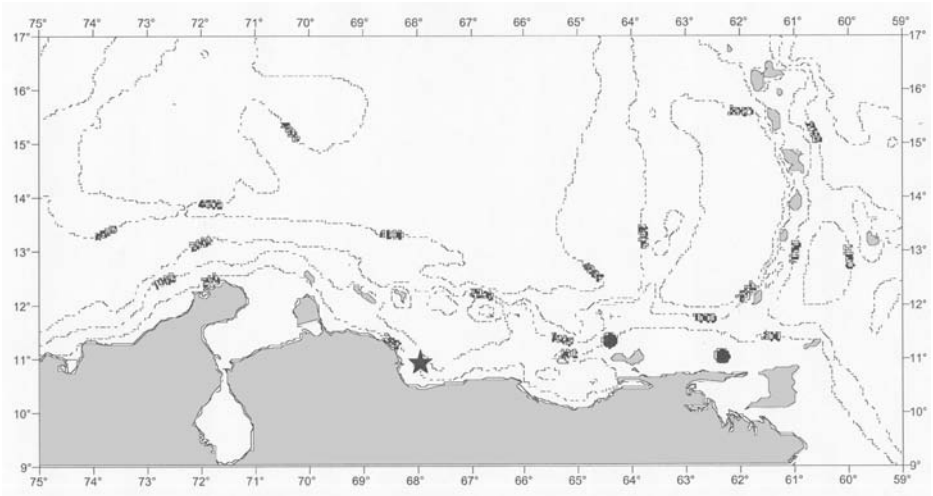


Figure 4. Geographical distribution of *Nematolampas venezuelensis* n.sp. Holotype: star; Paratypes: filled circles.

strip of tissue, with the exception of the anal organ (Fig. 3E). Total of 127 photophores present on entire specimen.

Male with single genitalia, which is on the right side of visceral organs. All specimens were immature, but in the largest, the holotype, a short inconspicuous penis is present.

*Holotype*.—Male ML 87.5 mm, U.S. National Museum of Natural History, USNM 817596.

*Type locality*.—Northeast of Golfo Triste, Venezuela. 10°55'N, 67°57'W, December 2, 1988, 371–383 m, bottom trawl.

*Distribution*.—*Nematolampas venezuelensis* is known only from the waters off the coasts of Venezuela between 10–12° N and 64–68° W (Fig. 4). All specimens were caught near the bottom during the night at 298–385 m, where bottom temperatures were 12–15° C.

*Etymology*.—The specific name *venezuelensis* is given after the country from whose waters the specimens were found.

## DISCUSSION

*NEMATOLAMPAS VENEZUELENSIS*.— The four male *N. venezuelensis* specimens examined in this study were all immature and collected in three different trawl stations off Venezuela. Because the purpose of the R/V NANSEN research cruises, during which the specimens were taken, was to survey demersal fishery resources (Anon., 1989) and not to collect specimens for scientific study, the majority of the cephalopods taken were badly damaged. In addition, most of the specimens were held frozen prior to permanent preservation in 70% ethanol at the laboratory. Only the holotype, was fixed in 10% formalin immediately after capture and subsequently transferred to 70% ethanol. Nonetheless, the four specimens of *N. venezuelensis* were in sufficiently good condition to determine the distinctive characters needed to verify a new species.

*Nematolampas regalis*, known only from Berry's original two specimens (Berry, 1913, 1914) is closely related to the new species. An examination of Berry's specimens (the



holotype body in good condition, portion of arms missing) showed them to be males, and a comparison of the two species showed them to share greatly elongated ventro-lateral arms with threadlike distal portions devoid of suckers (now left arm only present in holotype of *N. regalis*); ten similarly placed photophores within the mantle cavity; five photophores arranged on one row on the ventral periphery of each eye; single male genitalia; and no modification on the ventral arms that would indicate hectocotylization. *Nematolampas regalis*, differs in the presence of one photophore near the tip of each dorsal and dorso-lateral arm, in contrast to *N. venezuelensis*, in which only the dorso-lateral arm pair bears photophores, which are embedded in the dermal layer in the proximal third, and the dorso-lateral arms attenuate distally into a filament, a condition absent in *N. regalis* for this arm pair. Additionally, a pair of photophores are found on the ventral surface of the mantle near the posterior end of body at the attachment points of the posterior edges of the fins to the mantle in *N. regalis*, an arrangement absent in *N. venezuelensis*. Also, the elongated posterior end of the mantle in *N. venezuelensis* displays a distinctive large photophore embedded in the musculature of the fin/mantle complex and five bead-like, serially arranged photophores, features absent in *N. regalis*. The number of photophores on each ventro-lateral (III) arm in *N. regalis* exceed 31, in contrast to *N. venezuelensis* which has 19 photophores on each arm III. The 32 mm ML holotype of *N. regalis* was a mature male with the Needham sac full of spermatophores. No signs of hectocotylization were observed on either the ventral or dorsal arms. The largest male of the new species, the 87.5 mm-ml holotype, showed no evidence of advanced maturity, or of hectocotylization. These findings indicate that *N. regalis* males mature at a much smaller size than *N. venezuelensis*.

OVERVIEW OF THE FAMILY.—Examination of representatives of five of the six species known to occur in the Lycoteuthidae (see comparative material) yields a better understanding of the relationships within the family. The six species can be differentiated by the characters presented in Table 2. *Lampadioteuthis megaleia* is separated from the rest of the species by its unique form of the gladius, which has diamond-shaped, broad vanes with anterolateral borders slightly concave and a conus with a terminal acute rostrum as also observed in earlier studies (Young, 1964; Toll, 1983). Hess (1987) also found that spermatophore morphology separated *L. megaleia* from the other species. Other distinctive features include the presence of a hectocotylus on the right ventral arm and the distinct pattern of the photophores in the mantle cavity, and on the eyes and tentacles. Several authors have suggested (Voss, 1962; Young, 1964; Nesis, 1987) that the single male genitalia present in *L. megaleia* was an additional character that helped separate this species into a separate subfamily within the Lycoteuthidae. The findings of the present study disprove this proposed difference as both species of *Nematolampas* also have single male genitalia. Regardless, the remaining distinctive characters of this species, including differences in photophore arrangement, continue to support its separation into the subfamily Lampadioteuthinae.

With the addition of *N. venezuelensis*, the subfamily Lycoteuthinae now comprises three genera and five species (Table 2). *Lycoteuthis diadema* was first described by Chun (1900) as *Enoploteuthis diadema*, but in 1903 he placed this species in Pfeffer's genus *Lycoteuthis*. Later, in 1912, Chun's specimens were shown to be identical to Pfeffer's type *Lycoteuthis jattai* Pfeffer, 1900, which Pfeffer (1912) considered "jattai" to be a "museum name" and abandoned it (Vecchione and Young, 1999). Voss (1958, 1962) demonstrated that Pfeffer's paralarval *Astenoteuthion planctonicum* and Robson's



Table 2. Characters used in separating the species of the Family Lycoteuthidae.

| SubFamily/<br>Character                   | <i>Lycoteuthis lorigera</i>  | <i>Lycoteuthis springeri</i>   | <i>Nematolampas regalis*</i>   |
|---|--|--|--|
| Arms II                                   | Very long  | Very long  | Not Long   |
| Arms III                                  | Long   | Long   | Very long  |
| Arms IV in males                          | Not hectocotylized   | Not hectocotylized   | Not hectocotylized   |
| Gladius                                   | Vanes of gladius constricted medially to form an hourglass shape. Vane terminates in cup shaped cone | Vanes of gladius constricted medially to form an hourglass shape. Vane terminates in cup shaped cone | Vanes of gladius constricted medially to form an hourglass shape. Vane terminates in cup shaped cone |
| Photophores on tentacle                   | two, one at base of tentacle, one at base of carpus  | two, one at base of tentacle, one at base of carpus  | two, one at base of tentacle, one at base of carpus  |
| Photophores on arms                       | 52 photophores in arms II and 18 photophores in dorsal surface of arms III in males                  | 30+ photophores in arms II and 16 photophores in dorsal surface of arms III in males                 | one photophore in tips of arms I and II, and 62+ photophores in arms III in males                    |
| Photophores on tale or fin/mantle complex | Absent   | eight in males, one in females   | two in males, in ventral side near apex of mantle  |
| Ocular photophores                        | five serially arranged on ventral periphery  | five serially arranged on ventral periphery of eye, two on opposite corner of eyelid                 | five serially arranged on ventral periphery  |
| Photophores in mantle cavity              | two round anal, three anterior abdominal, two branchial, three posterior abdominal                   | two round anal, three anterior abdominal, two branchial, three posterior abdominal                   | two round anal, three anterior abdominal, two branchial, three posterior abdominal                   |
| Total photophores                         | 94   | 105+   | 92+  |
| Tail in mantle                            | Absent   | Present (long)   | Absent   |
| Genitalia in male                         | Paired   | Paired   | Single   |
| Size at maturity                          | Male: 155–187 mm Female: 113 mm  | Male: 80–98 mm Female: 125 mm  | Male: 32 mm  |
| Geographic Distribution                   | Oceans from the Southern Hemisphere  | Northwest Atlantic   | Off New Zealand  |

Table 2. Continued.

| SubFamily/<br>Character                   | Lycoteuthinae  |  | Lampadioteuthinae   |  |
|---|--|--|---|--|
|   | <i>Nematolampas venezuelensis</i> *  | <i>Selenoteuthis scintillans</i>   | <i>Lampadioteuthis megaleia</i>   |  |
| Arms II                                   | Long   | Not long   | Not long  |  |
| Arms III                                  | Very long  | Not long   | Not long  |  |
| Arms IV in males                          | Not hectocotylized   | Not hectocotylized   | Right arm hectocotylized  |  |
| Gladius                                   | Vanes of gladius constricted medially to form an hourglass shape. Vane terminates in cup shaped cone | Vanes of gladius constricted medially to form an hourglass shape. Vane terminates in cup shaped cone | Diamond-shaped broad vanes, anterolateral borders concave, conus with acute rostrum   |  |
| Photophores on tentacle                   | two, one at base of tentacle, one at base of carpus  | three, one at base of tentacle, one in mid tentacle, one at base of carpus                           | five, approximately equally spaced from base of tentacle to base of carpus            |  |
| Photophores on arms                       | 18 photophores in arms II and 38 photophores in arms III in males                                    | Single photophore at tips of arms II and III in males  | Absent  |  |
| Photophores on tale or fin/mantle complex | six in male, One large in fin/mantle complex and five smaller ones on short tail                     | One large globular at tip of posterior end of mantle in both sexes                                   | Absent  |  |
| Ocular photophores                        | five serially arranged on ventral periphery  | five serially arranged on ventral periphery  | four serially arranged on ventral periphery, one behind edge of pupil                 |  |
| Photophores in mantle cavity              | two round anal, three anterior abdominal, two branchial, three posterior abdominal                   | two round anal, three anterior abdominal, two branchial, three posterior abdominal                   | two round anal, two ellipsoidal anterior abdominal, and one round posterior abdominal |  |
| Total photophores                         | 127  | 29   | 23  |  |
| Tail in mantle                            | Present (short)  | Absent   | Absent  |  |
| Genitalia in male                         | Single   | Paired   | Single  |  |
| Size at maturity                          | Male: >87.5 mm   | Male: 32.5 mm Female: 30 mm  | Male: 31 mm Female : >30 mm   |  |
| Geographic Distribution                   | Caribbean Sea off Venezuela  | Northwest Atlantic   | Off New Zealand and Northeast Atlantic  |  |

\* Adult females not known.

*Leptodontoteuthis inermis* belongs in the synonymy of *L. diadema*. *Oregoniateuthis springeri* Voss, 1956 characterized by having elongate dorso-lateral arms and an elongate tail, was found to be the sexually dimorphic male of *L. diadema* (Toll, 1983).

Toll (1983) determined that the species described by Steenstrup in 1875 as *Onychoteuthis loligera* was a male with the basic proportions of a male *L. diadema*. The type specimen (180 mm–ML), which was in poor condition (Voss, 1962), had as type locality the ‘South Sea’. Forch and Uozumi (1990) redescribed *L. lorigera* from a single male and found that it lacked the long tail characteristic of *L. diadema*, and the females collected were indistinguishable from *L. diadema*.

Later, in a cephalopods study of the cephalopods of the Benguela Current off Namibia, Villanueva and Sanchez (1993) examined a number of *L. lorigera* of both sexes, all of which were mature specimens, and argued that *L. lorigera* males are con-specific with *L. diadema* females, based on indirect biological evidence in which *L. lorigera* males are found with *L. diadema* females in different areas of the southern hemisphere: off New Zealand (Förch and Uozumi, 1990) and in the Benguela Current off Namibia. Based on geography, *L. diadema* is assumed to be a synonym of *L. lorigera*, and the North Atlantic ‘*L. diadema*’ is *L. springeri*.

Although, no specimens of *L. lorigera* were examined in the present study, the author is inclined to believe like Nesis (1987), Villanueva and Sanchez (1993) and Vecchione and Young (1999) that *L. lorigera* is the species described by Chun (1910) as *Thaumtolampas diadema* (= *L. diadema*), and that *L. springeri* is the species with the mantle drawn out into a short tail in females and a long tail in males, bearing a single large photophore in the musculature at the apex of the fins in females, and eight slender, rodlike photophores in the tail of males (Voss, 1956, 1962; Toll, 1983).

Both species of *Lycoteuthis* can be differentiated from other members of the family by the long dorso-lateral arms in males. Females cannot be easily differentiated because of the presence of a light organ at the end of mantle in *L. springeri*. Because females of *Nematolampas* are not known, the separation of *Lycoteuthis* females from other members of the family remains unclear.

*Selenoteuthis scintillans* Voss, 1958 is well separated from the other species by the presence of a large globular photophore at the posterior end of mantle in both sexes and three photophores on the tentacles (Herring et al., 1985). Male specimens also can be separated by the absence of long lateral arms and the presence of a single photophore at tips of arms II and III.

The high level of sexual dimorphism in the family has been noted by several authors (Voss, 1962; Toll, 1983; Nesis, 1987; Villanueva and Sanchez, 1993). Examination of male specimens in five of the six species in the family and study of the literature showed that a hectocotylus is present in the single species of the subfamily Lampadioteuthidae, and absent in the five species of the subfamily Lycoteuthinae. Within the Lycoteuthinae, the males of *Lycoteuthis* have very long dorso-lateral arms and the males of *Nematolampas* have very long ventro-lateral arms, both genera with modified distal portions, which may be called ‘secondary sexual modification’ [perhaps of use in caressing or holding the females, as proposed by Voss (1980) in the Cranchiidae]. In contrast, the only known species of *Selenoteuthis* does not have elongated lateral arms. The Lycoteuthinae genera also differ in the photophore pattern on the lateral arms. In *Selenoteuthis*, a single photophore is present on the tip of each arm II and III, while in *Lycoteuthis* and *Nematolampas* several photophores are present in dorso- and ventro-lateral arms. In addition, males of

*Lycoteuthis* and *Selenoteuthis* have paired genitalia, in contrast to *Nematolampas*, which have single male genitalia.

Other features that heighten the level of sexual dimorphism in the family are the locations, arrangements and sizes of the photophores on the arms and body. As these squids are mesopelagic to benthic-bathyal (Nesis, 1987), one of the functions of these photophores may be to differentiate sexes (and probably species) at time of courtship. Herring et al. (1985) suggested the tail photophores may be used as specific sexual signaling organs.

The present study enhances our knowledge of the Lycoteuthidae with the addition of the new species to the family and reviews the characters that distinguish the species within the family. A full review of the family is needed to understand the position of the Lycoteuthidae in the teuthoid classification, but must await additional material of both sexes, in particular mature specimens.

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